Andvakia discipulorum, A New Species of Burrowing Sea Anemone from Hawai'i, with a Revision of *Andvakia* Danielssen, 1890[1]

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Abstract: We describe *Andvakia discipulorum* Daly & Goodwill, n. sp., from an intertidal mudflat of Kāne'ohe Bay, O'ahu, Hawai'i. Members of this species are inconspicuous, being small and having a column covered with sand. In comparison with other species of the genus, *Andvakia discipulorum*, n. sp., presents distinct arrangement of mesenteries, sizes of nematocysts, and musculature. We also provide a redescription of *Andvakia boninensis* based on specimens collected from Saipan, Mariana Islands. These descriptions provide an opportunity to revise and update the taxonomy of *Andvakia* and to address the systematics of family Andvakiidae. We determine that *Andvakia* is the senior synonym of *Decaphellia* and reject earlier hypotheses of synonymy between *Andvakia* and *Capneopsis*, *Ilyactis*, and *Octophellia*. A tabular key to the species of *Andvakia* is provided.

MEMBERS OF THE actiniarian genus *Andvakia* Danielssen, 1890, are small, sand-encrusted burrowing anemones. Because of their habitat, size, and morphology, these animals are quite cryptic and are thus not frequently collected or reported in the literature. Nonetheless, these animals cannot be considered uncommon, because they have been reported from shallow and shelf depths in all major ocean basins and may be locally abundant (Carlgren 1921, 1942).

Here we describe a new member of this genus, *Andvakia discipulorum* Daly & Goodwill, n. sp., from an intertidal mudflat in Hawai'i and redescribe *A. boninensis* Carlgren, 1943, based on a large sample of animals from Saipan, Mariana Islands. This is the first time since its description that *A. boninensis* has been reported in the scientific literature and the first time that living specimens have been described. These descriptions provide an opportunity to address the systematics of *Andvakia*. As Carlgren (1921) pointed out, Danielssen's (1890) original description of the genus was broad and neglected to mention key attributes, including the mesogleal marginal sphincter and acontia. Carlgren (1921, 1949) further noted that the genus was suspiciously similar to a number of other genera of burrowing actiniarians, including *Capneopsis* Duchassaing & Michelotti, 1864; *Ilyactis* Andres, 1883; and *Octophellia* Andres, 1883. In addition, it resembles *Decaphellia* Bourne, 1918; this resemblance was not noted by Carlgren (1949), who classified *Decaphellia* as a member of "Thenaria" (or Basilaria) despite its absence of basilar muscles, which are the diagnostic features of Thenaria. In addition to this taxonomic confusion, there has been nomenclatural confusion: the name of the genus has been misspelled many times (Carlgren 1921, 1942, 1943, 1949, Carlgren and Hedgpeth 1952), appearing more frequently as the incorrect "*Andwakia*" than the correct *Andvakia*.

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MATERIALS AND METHODS

Specimens were collected by hand from the intertidal and shallow subtidal zones. Living specimens were allowed to settle in aquariums containing sediment similar to that of the original habitat and were photographed once expanded. Densities of organisms were extrapolated to densities per square meter based on counts made with a small quadrat; because the animals were distributed in patches smaller than a square meter, the extrapolated density of animals exceeds the number observed in any patch. Specimens were fixed in 10% formalin or preserved in 95% ethanol; formalin-fixed specimens were transferred to 70% ethanol after a month or more. Type and voucher specimens have been deposited at the University of Kansas Natural History Museum and Biodiversity Research Center (KUNHM) and the U.S. National Museum of Natural History (Smithsonian Institution) (USNM).

Formalin-fixed specimens were examined whole, in dissection, and as serial sections. Serial sections were prepared using standard paraffin techniques. Histological slides were stained in Masson's trichrome (Presnell and Schreibman 1997). Small pieces of tissue from tentacles, column, pedal disk, mesenterial filaments, and actinopharynx were smeared on a slide; nematocysts in these smears were examined using Differential Interference Contrast at 1,000× magnification. Because of the small number of specimens of *A. discipulorum*, n. sp., and because their small size meant that making cnidae preparations destroyed much of the specimen, we have measured cnidae from all tissues of only two specimens. The small number of specimens examined precludes statistical interpretation of the size ranges of the cnidae. We use the cnidae terminology of Mariscal (1974) but have followed Carlgren (1940, 1943, 1949, 1951) and Carlgren and Hedgpeth (1952) in calling the large mastigophores of the filaments and acontia microbasic amastigophores, and the smaller mastigophores of the filaments microbasic *p*-mastigophores, although the distinction between these types is not always clear in undischarged capsules (Östman 2000).

We have based our diagnoses of higher taxa on those of Carlgren (1949), rendering them telegraphic and eliminating redundancies; more substantive changes are indicated in *italics*. The changes we have made were verified by examining the type specimens of *Andvakia mirabilis* Danielssen, 1890, the type species of the genus (University of Bergen Zoological Museum; ZMBN 603). Carlgren (1949) used the ranks "tribe" and "subtribe" to refer to groups between suborders and families. We have corrected this incorrect application of ranks in our treatment of Andvakiidae.

SYSTEMATIC RESULTS

Order ACTINIARIA
Suborder NYNANTHEAE
Family ANDVAKIIDAE Danielssen, 1890

DIAGNOSIS. *Actiniaria* with elongate, cylindrical body divisible into physa, scapus, and capitulum. Physa rounded or flattened. Scapus may have cinclides. Sphincter mesogleal, long, usually strong. Not more than six pairs of perfect mesenteries; perfect mesenteries fertile, with well-developed filaments, strong retractor muscles, and acontia. *Two pairs of directives, each associated with a siphonoglyph*. Imperfect mesenteries small, sterile, without retractor muscles, *at least some* extend the length of the column, may have filaments and acontia. Acontia with basitrichs and microbasic amastigophores.

INCLUDED GENERA. *Andvakia* Danielssen, 1890; *Synandwakia* Carlgren, 1947.

REMARKS. We have substituted "Actiniaria" for "Athenaria" in the diagnosis of Andvakiidae in recognition of the questionable phylogenetic and taxonomic status of Athenaria (see Daly et al. 2002, 2003, 2008, and later in this section). We have not used the terms "macrocnemes" and "microcnemes" to refer to the mesenteries: although Carlgren (1949) indicated that *Andvakia* has microcnemes, the imperfect mesenteries of Andvakiidae have filaments and acontia (Bourne 1918, Carlgren

1921, 1942, 1951, Carlgren and Hedgpeth 1952). According to Stephenson (1928) and Carlgren (1949), microcnemes lack filaments. We have added information about siphonoglyphs and mesentery number to facilitate comparison with other genera.

The correct spelling of the family name is Andvakiidae, rather than Andwakiidae. Carlgren frequently misspelled the name of the family as Andwakiidae (e.g., Carlgren 1921, 1942, 1943, 1949, Carlgren and Hedgpeth 1952), presumably as a result of his misspelling of the name of the type genus. This misspelling is incorporated into the correct and valid name *Synadwakia* Carlgren, 1947, which Carlgren created for *Andvakia hozawai* Uchida, 1932, recognizing that this species differs from others in *Andvakia* in lacking tenaculi and in having more mesenteries distally than proximally.

Genus *Andvakia* Danielssen, 1890

Decaphellia Bourne, 1918:60.

DIAGNOSIS. *Andvakiidae* with the column divisible into physa, scapus, and capitulum. Scapus with tenaculi. Capitulum without spirocysts. Physa small, sometimes flattened. Tentacles more than 12. Five or six perfect and fertile pairs of mesenteries with very strong restricted (reniform) to circumscribed retractor muscles; imperfect mesenteries without *muscles*. Acontia usually few, *short*. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic amastigophores.

TYPE SPECIES. *Andvakia mirabilis* Danielssen, 1890, by monotypy (Fautin et al. 2007).

INCLUDED SPECIES. *A. boninensis; A. insignis* Carlgren, 1951; *A. isabellae* Carlgren & Hedgpeth, 1952; *A. mirabilis; A. parva* Carlgren, 1940; *Decaphellia psammomitra* Bourne, 1918.

REMARKS. Carlgren (1921, 1942, 1943, 1949, Carlgren and Hedgpeth 1952) misspelled the genus as *Andwakia*, an incorrect subsequent spelling of *Andvakia* Danielssen, 1890 (ICZN [1999]: Article 33.3; see Fautin et al. [2007]).

Andvakia boninensis Carlgren, 1943

Figures 1, 2; Table 1

Andwakia boninensis Carlgren, 1943:23–24.
Andwakia boniensis Carlgren, 1949:39.

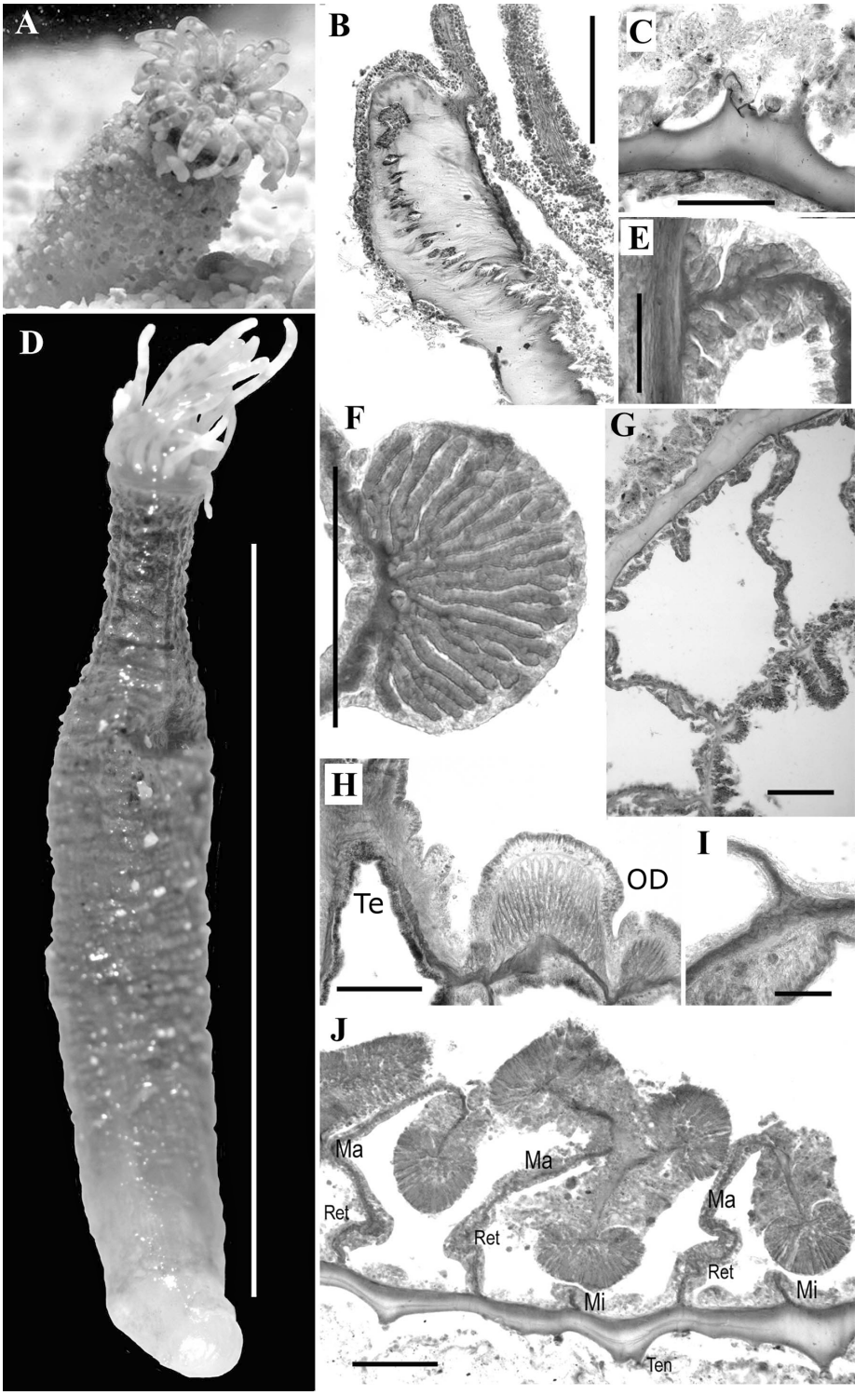
DIAGNOSIS. With 24 tentacles; elongate, vermiform body covered with fine sand; larger particles adhere to small tenaculi. Length of slightly contracted specimens 14–20 mm, diameter 2–3 mm.

MATERIAL EXAMINED. Pacific Ocean: Mariana Islands: Saipan: Puerto Rico mudflat, KUNHM 2965 (6 specimens) and KUNHM 2966 (9 specimens); San Antonio Beach, KUNHM 2964 (6 specimens); and Tanapag Beach, KUNHM 002710 (2 specimens), 002711 (1 specimen).

EXTERNAL ANATOMY. Column divisible into physa, scapus, scapulus, and capitulum; periderm covers scapus and scapulus (Figure 1*A*, *D*). Capitulum greenish gray, streaked with opaque white between mesenteries, with tan splotches at junction with tentacles. Scapus beige to brown in life, without cinclides, bearing small tenaculi to which larger grains of sand adhere (Figure 1*A*, *C*, *D*). Physa ampullaceous, translucent white. Preserved specimens uniform beige. Fully contracted specimens ovoid to spherical.

Oral disk circular, concave between tentacles and prominent hypostome, translucent white, with irregular opaque white and brown chevrons between mesenterial insertions (Figure 1*A*); color fades over time in specimens stored in alcohol. Musculature of oral disk strong, ectodermal (Figure 1*H*). Tentacles marginal, short, bluntly tapering, 24, in two cycles of 12 (Figure 1*A*), those of outer cycle shorter. In life, tentacles translucent white with irregularly spaced opaque white and brownish gray chevrons on oral surface (Figure 1*A*).

INTERNAL ANATOMY AND HISTOLOGY. Two cycles of six pairs of mesenteries, each extending length of column: first cycle perfect, fertile; second cycle imperfect, without musculature (Figure 1*J*). Additional cycle of very small imperfect mesenteries at proximal end of column; these do not bear acontia,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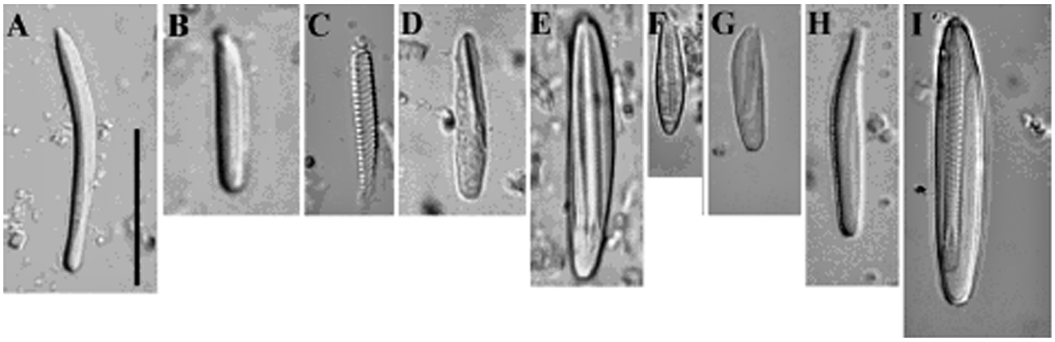

FIGURE 2. Cnidae of *Andvakia boninensis* Carlgren, 1943, and *Andvakia discipulorum*, n. sp. The capsules of the two species differ only in size. Scale bar = 15 μm. *A.* Large basitrich of tentacle. Cnidae of similar morphology found in actinopharynx. *B.* Small basitrich of tentacle. Cnidae of similar morphology found in filament. *C.* Spirocyst. *D.* Small microbasic *p*-mastigophore of actinopharynx. *E.* Large microbasic *p*-mastigophore of actinopharynx. *F.* Microbasic *p*-mastigophore of filament. *G.* Microbasic *p*-mastigophore of filament. The cnidae depicted in *F* and *G* are identical in size but have slightly different capsule morphologies; these could not be distinguished consistently and thus are not distinguished in Table 1. *H.* Basitrich of acontia. Note distinctive "neck" at the distal end of the capsule. *I.* Microbasic amastigophore of acontia.

muscles, or filaments. Each perfect mesentery with small oral stoma. Marginal sphincter mesogleal, relatively short, with large lacunae centered in mesoglea or slightly closer to epidermis distally, tapering toward gastrodermis proximally (Figure 1*B*). Parietal and retractor muscles circumscript, relatively strong (Figure 1*E*, *F*), only on perfect mesenteries below actinopharynx (Figure 1*G*, *J*). Parietal muscle symmetrical, without separate pennon (Figure 1*E*). Acontia short, not tightly coiled, arise from imperfect mesenteries at midcolumn and from perfect mesenteries proximally. Basilar muscles absent (Figure 1*I*).

CNIDOM. Spirocysts, basitrichs, microbasic amastigophores, microbasic *p*-mastigophores (Figure 2; see Table 1 for size and distribution).

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. Specimens collected from three areas on Saipan, Mariana Islands: San Antonio Beach Park reef flat, Puerto Rico mudflat, and Tanapag Beach Park sand flat. At San Antonio, all specimens were found in shallow subtidal zone (0.3–0.9 m), attached to hard rock substrate covered with several millimeters of sand but never attached to loose rocks. The anemones were not numerous (one or two per square meter) and occurred singly. Because members of this species are cryptically colored and nocturnal, they cannot be found by visual inspection of the sand

FIGURE 1. Anatomy and histology of *Andvakia boninensis* Carlgren, 1943. *A.* Partially expanded living specimen. Note large mouth atop hypostome. *B.* Longitudinal section through distal column, showing mesogleal marginal sphincter muscle. Scale bar = 150 μm. *C.* Columnar tenaculum. The epidermis has been damaged by the removal of adherent material. Scale bar = 25 μm. *D.* External anatomy, partially expanded preserved specimen. Scale bar = 10 mm. *E.* Cross section through perfect mesentery showing parietal muscle. Scale bar = 25 μm. *F.* Cross section through perfect mesentery showing retractor muscle. Scale bar = 100 μm. *G.* Cross section through column at proximal end of actinopharynx, showing perfect and imperfect mesenteries. Scale bar = 150 μm. *H.* Longitudinal section through oral crown showing musculature of oral disk (OD) and a longitudinal section through a tentacle (Te). Scale bar = 150 μm. *I.* Longitudinal section through proximal column, showing junction of mesentery and base. Note absence of musculature. Scale bar = 25 μm. *J.* Cross section through column below actinopharynx, showing perfect (Ma) and imperfect (Mi) mesenteries. Retractor muscles (Ret) are on perfect mesenteries only; parietal muscles are not visible at this magnification. Although much of the epidermis has sloughed off, mesoglea of tenaculum (Ten) remains visible. Scale bar = 250 μm.

TABLE 1

Cnidae of *Andvakia boninensis* Carlgren, 1943, and *A. discipulorum*, n. sp.

	A. boninensis			*A. discipulorum*, n. sp.	
Parameter	Carlgren (1943)	Range	*n*	Range	*n*
Tentacle					
Spirocysts		13.8–27.9 × 1.5–3.3	29	12.7–25.1 × 1.4–3.3	19
Large basitrichs	(18.3) 24–32.4 × ~2	22.6–39.2 × 1.7–2.9	52	19.9–32.8 × 1.3–2.5 (3.1)	58
Small basitrichs	11.3–13 × ~2	10.7–14.9 × 1.7–2.4	7	8.9–14.7 × 1.1–2.1	28
Actinopharynx					
Basitrichs		17.6–24.9 × 1.2–2.6	31	21.1–25.7 × 1.9–3.1	11
Microbasic *p*-mastigophores	21–25.4 × 4.2	19.7–27.0 × 3.0–4.6	41	25.0–28.2 × 3.6–5.6	14
Microbasic amastigophores		33.2–44.6 × 4.9–6.7	52	34.9–39.5 × 5.8–7.7	14
Filaments					
Basitrichs		9.9–13.3 × 1.5–2.1	12	7.4–14.6 × 0.8–2.0	31
Microbasic *p*-mastigophores	14–17 × 2.8–3.5	15–21.4 × 2.0–3.6 (3.9)	58	12.8–18.6 × 2.1–4.2	31
Acontia					
Basitrichs	17–21.2 × 2	15.2–23.4 × (1) 1.4–2.4	40	12.7–24.6 × 1.0–2.3	71
Microbasic amastigophores	35.2–50 × 5.6–7.7 (8.5)	(37) 39–62.2 × 4.0–8.1	45	31.3–45.9 × 5.3–8.3	45

Note: Capsules are depicted in Figure 2. Sizes are given as ranges of length and width; measurements of exceptionally large or small capsules are in parentheses. Measurements from Carlgren (1943) for *A. boninensis* are included for comparison. Carlgren did not report sizes for all types of cnidae from all tissues; the cells corresponding to types not reported are left empty. *n* is the number of capsules measured. Capsules were measured from two specimens of *A. discipulorum*, n. sp., and three of *A. boninensis;* all types of cnidae were found in all specimens examined. It is possible that the small basitrichs of the tentacles and filaments of *A. boninensis* are from the same source and that their occurrence in one of the tissues is due to contamination. However, because they were found in each tissue in both specimens and were approximately equal in abundance in each tissue, the direction of contamination, if it occurred, cannot be determined.

surface during the day. However, at San Antonio, *A. boninensis* co-occurs with an unidentified diurnal anemone of the same size that was easily found by locating the unknown anemone's tentacles on the sand surface. Upon removal of the covering sand, the unknown anemone would quickly contract, whereas *A. boninensis* remained relatively uncontracted and thus conspicuous. In the laboratory, *A. boninensis* can rebury itself overnight if left exposed.

Specimens collected from Puerto Rico mudflat and Tanapag Beach Park were intertidal and not attached to a solid substrate but burrowed in the mud and sand. At Puerto Rico mudflat, the density of *A. boninensis* at some locations approximated 100/m^2, whereas on the Tanapag sand flat the density averaged only 7/m^2. In both places, they were widely spaced and not aggregated but co-occurred with the anemone *Edwardsianthus gilbertensis* (Carlgren, 1931), whose burrows were easy to spot and whose extrapolated aggregated density at some locations may be as high as 4,800/m^2.

Multiple specimens of *A. boninensis*, without the co-occurring *E. gilbertensis*, were found in a single dense aggregation in mud burrows in one section of a rusting World War II barge whose sections functioned as enclosed aquariums with water exchange only during high tides. All 46 individuals in the aggregation were unattached to the substrate and spaced irregularly but closely together with neither tentacles nor columns touching.

REMARKS. No type specimens are known (Fautin 2007). Carlgren (1949) incorrectly spelled the species epithet, giving the name as *boniensis* rather than *boninensis*.

Andvakia discipulorum Daly & Goodwill, n. sp.
Figures 2, 3; Table 1

DIAGNOSIS. With 24 tentacles; elongate body covered with fine sand; larger particles adhere to small tenaculi. Length of slightly contracted specimens 6–12 mm, diameter 1.5–2 mm.

MATERIAL EXAMINED. Holotype: USNM 113966, Pacific Ocean: He'eia Kea mudflat, Kāne'ohe, O'ahu, Hawai'i. Paratypes: USNM 3967 (4 specimens plus slides), collected at same locality as holotype.

EXTERNAL ANATOMY. Column divisible into physa, scapus, scapulus, and capitulum; periderm covers scapus and scapulus (Figure 3*A*, *B*). Capitulum translucent white, with faint brown streaks between mesenteries in some specimens. Scapus beige to brown in life, without cinclides, with fine periderm and sparsely scattered tenaculi to which larger grains of sand adhere (Figure 3*A*, *B*, *H*); scapulus distinguished from scapus in lacking tenaculi and adherent particles. Periderm thicker, looser distally. Preserved specimens uniform beige. Ampullaceous physa translucent white. Aboral end rounded or flattened, adheres to small stones. Fully contracted specimens ovoid to spherical.

Oral disk narrow, without prominent mouth, with strong furrows indicating mesenterial insertions. Oral disk strongly patterned with alternating brown and opaque white chevrons (Figure 3*C*). Distinct white splotches mark base of tentacles associated with directive endocoels. Oral disk musculature ectodermal, weak, not well differentiated from mesoglea. Tentacles marginal, blend into oral disk, bluntly tapering, 24, in two cycles of 12, those of outer cycle shorter (Figure 3*B*, *C*). In life, tentacles translucent white with irregularly spaced opaque white and brown chevrons on oral surface (Figure 3*B*, *C*); chevrons more widely spaced toward tips of tentacles.

INTERNAL ANATOMY AND HISTOLOGY. Two cycles of six pairs of mesenteries extend length of column: five pairs of first cycle perfect; sulcolateral (= ventrolateral) pair of first cycle imperfect; all members of second cycle imperfect, small, without muscles but with filaments and acontia. Marginal sphincter mesogleal, weak; relatively short band of small lacunae lie closer to epidermis, tapering slightly distally and proximally (Figure 3*D*, *E*). Parietal and retractor muscles on perfect mesenteries only. Retractor muscle circumscript, strong (Figure 3*F*). Parietal muscle symmetrical, very weak, without separate pennon (Figure 3*G*). Acontia short, not tightly coiled, arise from imperfect mesenteries at midcolumn and from perfect mesenteries proximally.

CNIDOM. Spirocysts, basitrichs, microbasic amastigophores, microbasic *p*-mastigophores (Figure 2; see Table 1 for size and distribution).

ETYMOLOGY. The species epithet is the genitive case of the Latin noun "*discipulus*" and can be translated "of the students." This name recognizes the Brigham Young University Hawai'i students who discovered the first several specimens on field trips to Kāne'ohe Bay.

DISTRIBUTION, HABITAT, AND NATURAL HISTORY. Specimens were collected from He'eia Kea mudflat of Kāne'ohe Bay, O'ahu, Hawai'i. Animals were only found during a single trip; they were not seen on repeat visits to the same site nor on visits to similar habitats. All were intertidal (subtidal search not conducted) and attached to small to medium-sized rocks, most of which were buried in the mud. All specimens were found by examining all surfaces of haphazardly collected rocks. All specimens of *A. discipulorum*, n. sp., were attached to different rocks: no rocks bearing multiple specimens were found. Collected specimens were not tightly attached to the rock surface and frequently detached when the rock was moved.

DISCUSSION

Differential Diagnosis of Species

All described species of *Andvakia* are similar in external anatomy. Although most species burrow, at least three species live attached to small stones or shells (Table 2; see also

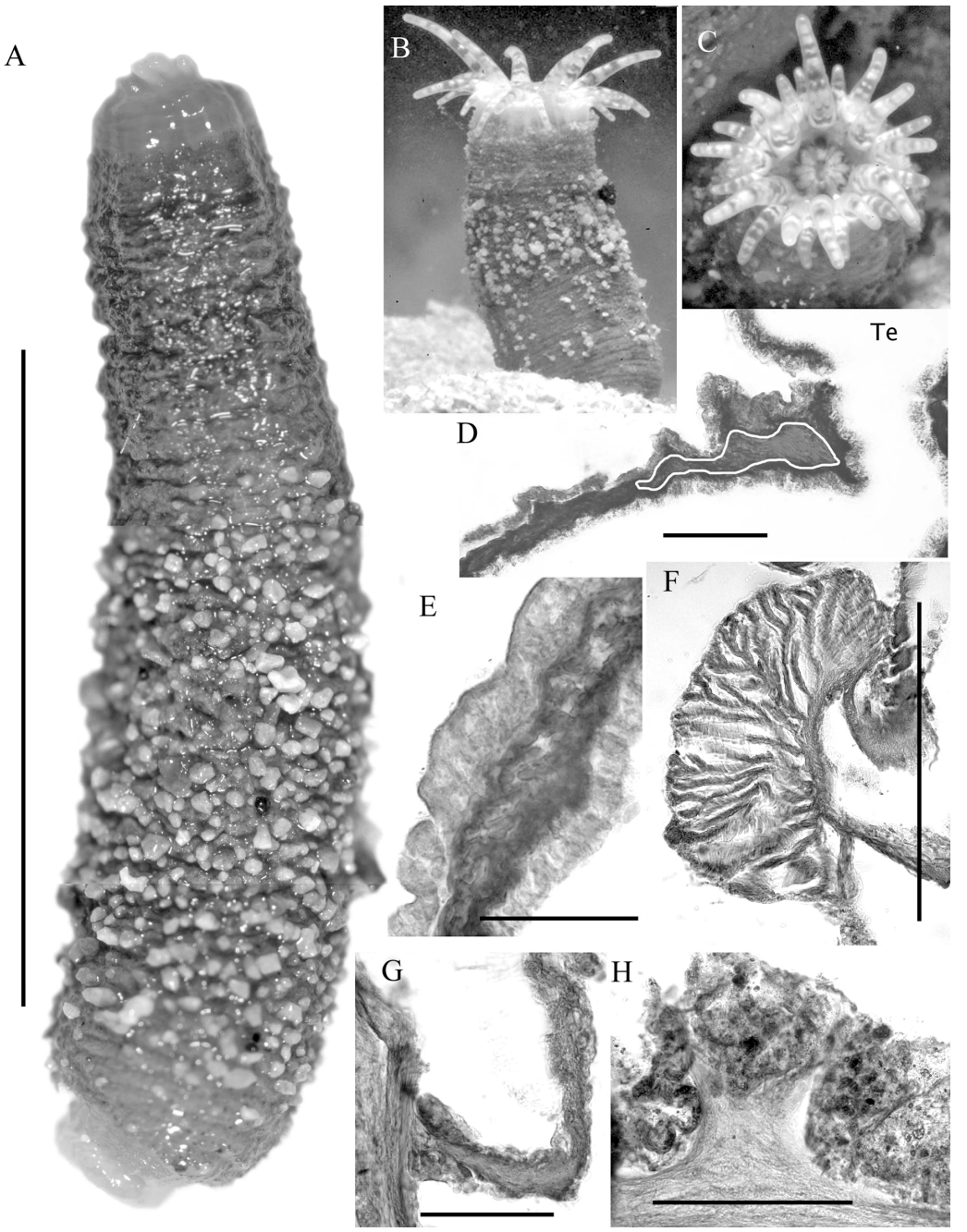

FIGURE 3. Anatomy of *Andvakia discipulorum* Daly & Goodwill, n. sp. *A.* External anatomy, contracted specimen. Scale bar = 5 mm. *B.* Lateral view of expanded living specimen in substrate. Periderm-free capitulum is visible just below oral crown. *C.* Oral view of partially expanded living specimen. *D.* Longitudinal section through distal column. Mesogleal marginal sphincter muscle is outlined in white; a tentacle (Te) is indicated for orientation. Scale bar = 0.50 mm. *E.* Close-up of small lacunae of marginal sphincter muscle. Scale bar = 25 μm. *F.* Cross section through perfect mesentery below actinopharynx showing retractor muscle. Scale bar = 100 μm. *G.* Cross section through perfect mesentery showing parietal muscle. Scale bar = 50 μm. *H.* Columnar tenaculum. Scale bar = 25 μm.

TABLE 2

Valid Species of *Andvakia* Danielssen, 1890

Andvakia species	Perfect Mesenteries	No. of Tentacles	Tenaculi	Musculature	Habit	Known Range
discipulorum, n. sp.	10, regularly arranged	24	Densest distally	Sphincter and parietal weak, retractor strong	Buried in sediment with aboral end attached to stones	Central Pacific Ocean: Hawai'i. Intertidal
boninensis	12	24	Scattered on scapus	Sphincter, parietal, and retractor strong	Buried in sediment with aboral end unattached or attached to solid substrate	Eastern Pacific Ocean: Bonin Islands; Western Pacific Ocean: Saipan, Mariana Islands. Intertidal and shallow subtidal
insignis	12	24	Densest distally	Sphincter, parietal, and retractor strong	Burrowing	Sea of Cortez. Depth unknown
isabellae	12	48	Densest distally	Parietal weak, retractor strong	Burrowing	Gulf of Mexico: Texas. <20 m
mirabilis	12	24	Scattered on scapus	Sphincter and parietal weak, retractor strong	Burrowing	North Atlantic Ocean: Sweden. Subtidal, 150–275 m
parva	10, irregularly arranged	20–24	Scattered on scapus	Sphincter, parietal, and retractor strong	Attached to shells and stones	North Atlantic Ocean: Sweden. Subtidal, 60 m
psammomitra	10 distally, 9 proximally	24	Densest distally	Parietal weak, retractor strong	Attached to shells and stones	Eastern Pacific Ocean: New Guinea. Intertidal

Carlgren [1942]). Species of *Andvakia* are similar in general internal anatomy, having one cycle of six pairs of perfect mesenteries, and reniform retractor muscles (Table 2). The species differ in the number of tentacles, development of the parietal and sphincter muscles, and sizes of the cnidae.

Andvakia discipulorum, n. sp., resembles *A. psammomitra* and *A. parva* in that some pairs of mesenteries in the first cycle are imperfect. In *A. parva*, the mesenteries are irregularly arranged, and the pairs that are imperfect differ between specimens, a condition Carlgren (1942) interpreted as evidence of regeneration. In *A. discipulorum*, n. sp., the sulcolateral pair is always imperfect. The sphincter muscle of *A. discipulorum*, n. sp., is much weaker than that of *A. parva*, comprising a short meshwork of small lacunae not visible except under high magnification (Figure 3*D*, *E*), and the tenaculi of *A. discipulorum*, n. sp., are noticeably denser distally. Finally, the two differ substantially in their distribution: *A. parva* has been reported from the North Atlantic and *A. discipulorum*, n. sp., is known from the central Pacific. Like *A. discipulorum*, n. sp., *A. psammomitra* is a tropical Pacific species, being reported from New Guinea. However, unlike *A. discipulorum*, n. sp., *A. psammomitra* has 10 perfect mesenteries distally, but only nine proximally, as one member of the dorsolateral pair is reduced proximal to the actinopharynx. Thus, *A. discipulorum*, n. sp., can be distinguished from all known species of *Andvakia* based on the arrangement of mesenteries, musculature, or external anatomy.

Andvakia boninensis has the same number of tentacles as *A. mirabilis* and *A. insignis*. *Andvakia mirabilis* is known only from the

North Atlantic and has weakly developed sphincter and retractor muscles (Table 2). *Andvakia insignis* and *A. boninensis* have similarly developed sphincter and retractor muscles but differ in the size of the cnidae: the basitrichs of the tentacles and acontia and the microbasic *p*-mastigophores of the acontia are larger in *A. boninensis*, and the microbasic *p*-mastigophores of the actinopharynx are wider in *A. insignis* (compare Table 1 and Carlgren [1951]).

Systematics of Andvakia

Carlgren (1949) suggested that *Andvakia* might be a junior synonym of *Capneopsis*, *Ilyactis*, and *Octophellia*. The single species of *Capneopsis*, *C. solidago* Duchassaing & Michelotti, 1864, is a member of the genus *Telmatactis* Gravier, 1916 (see Cairns et al. 1986, den Hartog 1995). The sole species of *Ilyactis*, *I. torquata* Andres, 1883, has not been reported since its original description, nor are any type specimens known. An identical situation pertains in *Octophellia:* the type species, *O. timida* Andres, 1883, has not been recorded since Andres' original description, and type material is unknown (Fautin 2007). For both *I. torquata* and *O. timida*, the descriptions are insufficient to differentiate the species from other burrowing anemones, and neither contains information relevant to placing the species within a currently valid family of Actiniaria. Thus, both *I. torquata* and *O. timida* are nomina nuda. The only other species ever assigned to *Octophellia* is *Phellia gausapata* Gosse, 1858, the type species of the genus *Phellia* Gosse, 1858, which differs from *Andvakia* in having basilar muscles. Thus, we regard *Andvakia* as the correct and valid name for the genus.

Bourne (1918) described the genus *Decaphellia* and its single species, *D. psammomitra*, from a single collection of specimens from New Caledonia. No specimens are known. Because his specimens were attached to small stones at their aboral ends and had basitrichs in the acontia, he placed them among the Phellinae, a subset of the "family Actinidae," a group whose membership more or less corresponds to the modern suborder Nynantheae. Because no other genus in this group had so few mesenteries or such an elongate column, Bourne (1918) created a new genus for the species. Carlgren (1949) did not question the validity or distinctness of *Decaphellia* and placed it in Isophellidae Stephenson, 1935, a group that included all former Phellinae with microcnemic mesenteries and both basitrichs and microbasic amastigophores (or *p*-mastigophores) in the acontia. Nonetheless, the diagnosis Carlgren (1949) gave for the family is wholly congruent with that of *Andvakia* (Table 3). Carlgren (1951) later discussed the difficulty of separating the genera of Andvakiidae from those of Isophellidae because of the similarity of the cnidae in the acontia and the difficulty of differentiating between parietal muscles and basilar muscles in small, vermiform animals but did not tie this observation to the diagnoses of *Andvakia* and *Decaphellia*. No specimens of *Decaphellia* are known, and thus the description is the only evidence of the genus or its sole species. Because we find no differences between the diagnoses of *Decaphellia* and *Andvakia* (Table 3), we regard *Decaphellia* as a junior synonym of *Andvakia*.

Relationships between the acontiate groups with basilar muscles and those without are unclear. Stephenson (1920) proposed that all acontiate forms had a single origin. Carlgren (1949) divided these taxa, grouping those with basilar muscles with the other forms having those muscles (in "Thenaria") and those without basilar muscles with other forms that lacked basilar muscles (in "Athenaria"). Hand (1961) noted that *Mimetridium* Hand, 1961, was more similar to members of the Haliactidae than it was to other members of its own family and proposed that all of the acontiate forms were closely related, with either the forms without muscles evolving basilar musculature or the forms with basilar muscles losing basilar musculature. Indeed, each of the groups without basilar muscles has at least one ally among the acontiate taxa with basilar muscles (Table 4). Of course, it is possible that both scenarios may apply, with some forms without basilar

TABLE 3

Comparison of the Diagnoses of *Andvakia* and *Decaphellia*

Feature	*Andvakia*	*Decaphellia*
Column distinctly divisible into regions	Yes	Yes
Tenaculi	On scapus	On scapus
Sphincter	Mesogleal: strong to weak	Mesogleal: weak
Tentacle number	>12	24
Siphonoglyph	Variable: indistinct	2
Pairs of mesenteries	Variable: usually 12	12
Pairs of macrocnemes	5–6	5
Retractor musculature	Circumscribed to restricted	Circumscribed
Parietal musculature	Few folds	Few folds
Mesenteries distally versus proximally	Same number	Same number
Acontia	Perfect and/or imperfect mesenteries	Imperfect mesenteries only?
Nematocysts of acontia	Basitrichs, microbasic amastigophores	Basitrichs, microbasic amastigophores
Other cnidae	Spirocysts, microbasic *p*-mastigophores	Unknown. No data

Note: Characters are those used by Carlgren (1949) in his diagnoses of the genera, with additional information from Danielssen (1890), Bourne (1918), Carlgren (1921, 1940, 1951), and Carlgren and Hedgpeth (1952).

TABLE 4

Comparison of Acontiate Lineages with and without Basilar Muscles

Without Basilar Muscles	With Basilar Muscles	Characteristics Shared
Andvakiidae	Isophellidae	Mesenteries of two sizes and morphologies Mesogleal sphincter Acontia with basitrichs and microbasic amastigophores
Haliactidae	Acontiophoridae	Mesenteries of two sizes and morphologies Sphincter absent Acontia with basitrichs and microbasic amastigophores
Octineonidae	Bathyphelliidae	Mesenteries of two sizes and morphologies Mesogleal sphincter Acontia with basitrichs only

Note: For each family of acontiate Athenaria, we have identified the family of acontiate Thenaria that is most similar in terms of the attributes generally used to identify major groups in Actiniaria.

muscles being phylogenetically basal to a larger acontiate clade that has evolved basilar muscles, and others being derived via loss of basilar muscles.

In the case of *Andvakia*, phylogenetic analyses of DNA sequence data clearly indicate an affinity with the acontiate Thenaria (Daly et al. 2008), suggesting that members of this group have lost basilar muscles. Sequences from nuclear 18S and 28S rDNA and from mitochondrial 12S and 16S rDNA concur that the included representative of Andvakiidae, *A. boninensis*, is more closely related to acontiate species like *Phellia gausapata* Gosse, 1858, than to basilar muscleless forms like *Edwardsia elegans* Verrill, 1869, *Halcampoides purpurea* (Studer, 1879), or *Haloclava producta* (Stimpson, 1856).

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